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A NEW SPECIES OF *PARALEPAS* (CIRRIPEDIA: HETERALEPADIDAE) SYMBIOTIC WITH *XENOPHORA* (MOLLUSCA: GASTROPODA); WITH THE FIRST COMPLEMENTAL MALE KNOWN FOR THE FAMILY

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ABSTRACT

A new species of *Paralepas* from near Madagascar is described and its affinities are indicated. A generalized complemental male and a male cyprid larva were found attached below the aperture in two specimens. This is the first male reported for this group of barnacles, and its morphological characters are investigated.

Twenty-two species of the genus *Paralepas* Pilsbry were reported in the last review of this genus (Zevina, 1982), and four have since been described. These latter are: *P. robusta* Rossel, 1981, from the Philippines; *P. seama* Foster, 1981, from New Zealand; *P. ichtiandri* Zevina, 1983, from Nasca Ridge (off the coast of Peru, 20°S, 80°W), and *P. martini* Young, 1990, off the coast of Brazil. The new species described here is from the Indian Ocean.

Species of *Paralepas* are restricted to the tropical and subtropical waters of the World Ocean, mostly between the subtidal and upper bathyal zones. These barnacles are often found in association with other organisms, such as mollusks, echinoids, and large crustaceans. No previous works have mentioned complemental males in *Paralepas*.

In the course of a survey of the collections at the Institution of Oceanology, Russian Academy of Sciences, three specimens of *Paralepas* new species, preserved in alcohol, were found. They were attached near the orifice of a gastropod belonging to the genus *Xenophora*. One adult specimen bears a complemental male, attached externally to the lower part of the orifice (Fig. 1C), and another has a cyprid larva attached in the same place (Figs. 1A,D). The juvenile has neither a male nor a cyprid larva.

MATERIALS AND METHODS

The slide preparations of the cuticle and "soft body" of the hermaphrodites were investigated using of monocular and stereo light microscopes.

The complemental male was separated from the adult and postfixed with 1% osmiumtetroxide solution and later dehydrated in an ethanol series and acetone, and embedded in Epon. Semi-thin sections (5–7 μm)were made with a glass knife using a Dupont Ultracut microtome and stained in 1% toluidine blue. These sections were examined by means of a Opton Axioskope stereo light microscope.

SYSTEMATICS

Heteralepadidae Nilsson-Cantell, 1921
Paralepas Pilsbry, 1907
Paralepas klepalae new species
Figures 1–3

Material Examined.—North of Madagascar: 12°29′S, 48°18′E, 380 m, 3 specimens (2-adults, 1-juvenile), attached outside (near the aperture) of one shell of *Xenophora* sp. (Gastropoda).

Deposition of Types.—The holotype (N Mg 1132) and two paratypes are deposited in the Zoological Museum of Moscow State University.

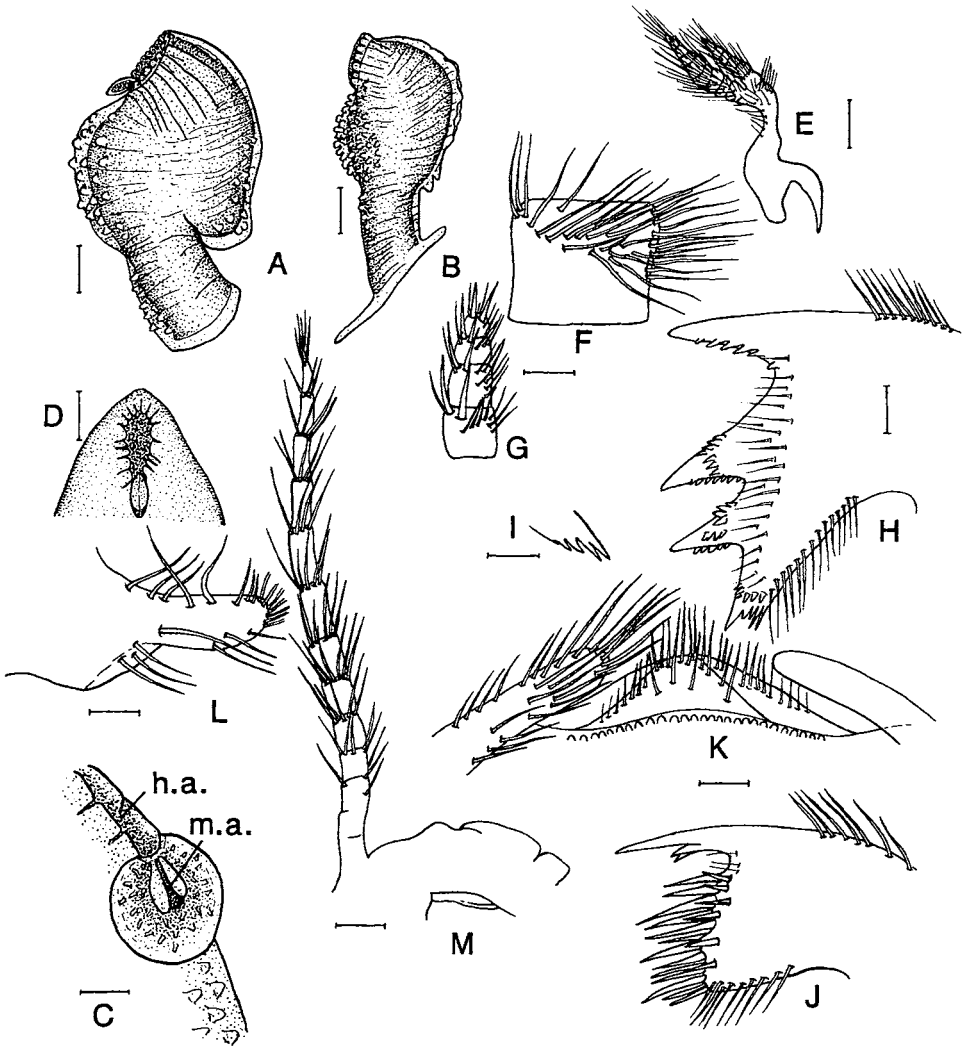

Figure 1. *Paralepas klepalae* new species. a. external view of adult specimen (holotype) with attached cyprid larva; b. external view of juvenile specimen; c. attached complemental male; d. apertural view of specimen (a) with the subapertural cyprid larva; e. cirrus I; f. 5th segment of anterior ramus of cirrus IV; g. distal segments of anterior ramus of cirrus III; h. mandible; I. lower angle of other mandible; j. maxilla I; k. labrum and palps; l. end of penis; m. a caudal appendage and the base of the penis. (Scale bars. a—1.7 mm; b,d—1 mm; c -0.33 mm; e,h,j,k—350 μm; f,g,i,l—100 μm; m—560 μm). Figures e-m belong to the specimen (a). c.l.—cyprid larva; h.a.—hermaphrodite aperture; m.a.—male aperture.

The Hermaphrodite.—DESCRIPTION. Capitulum broad-oval; length 6 mm, width 4.5 mm. Length of stalk 4.5 mm, diameter about 2.5 mm. Color in preservative light yellow. Cuticle thick, weakly wrinkled, with small tuberculate formations on the rostral and carinal sides of capitulum, and along rostral side of stalk. Holotype with swelling at basis of carinal side of capitulum and juvenile with some spines at same place. Orifice 1/3 or more length of capitulum , orifice lips wrinkled. MOUTHPARTS. Labrum with row of numerous, small, oval teeth below

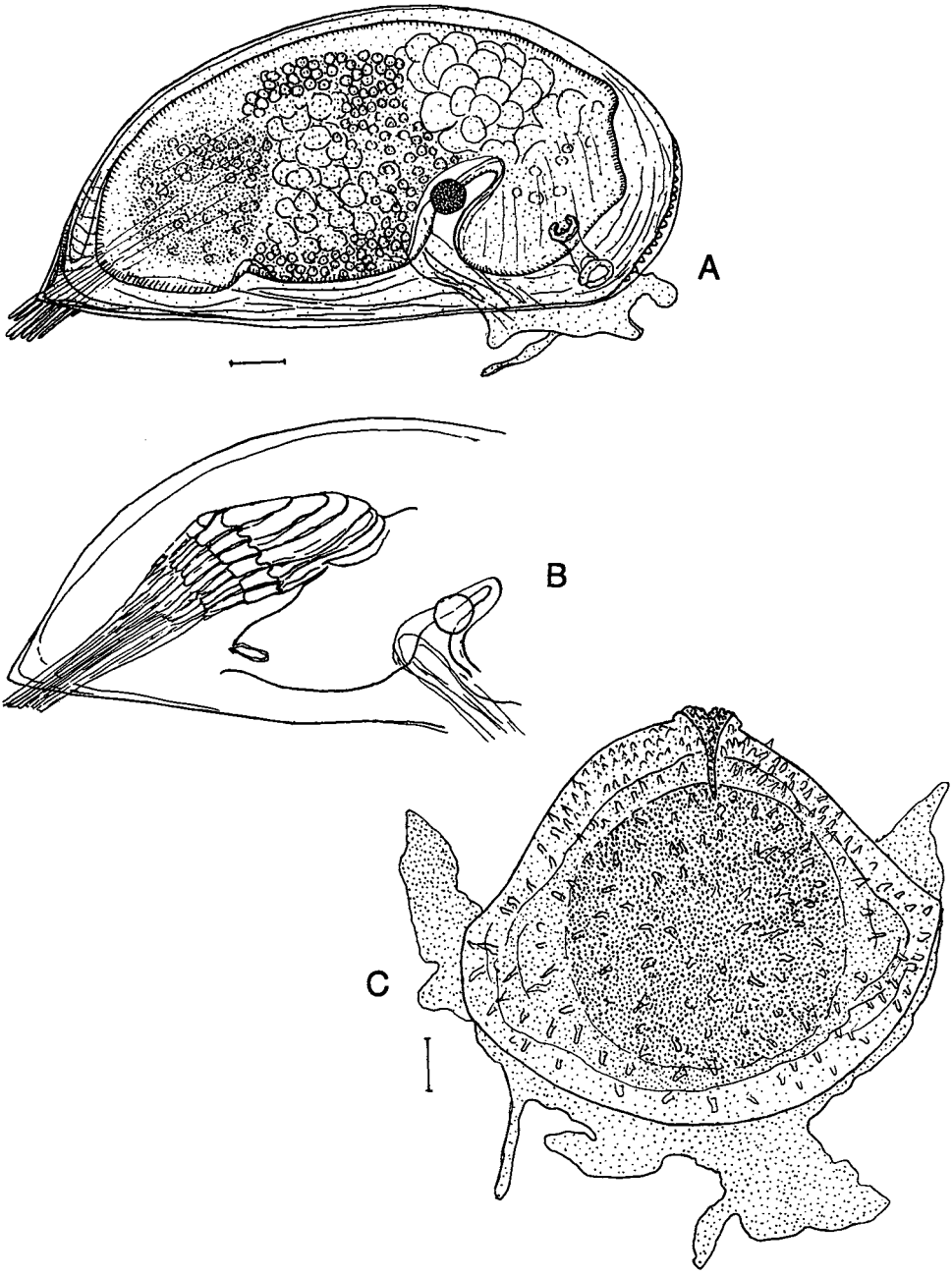

Figure 2. a. Cyprid larva of male, general view; b. posterior end of cyprid larva after treatment with KOH solution; c. complemental male (from fig. 1c), external view (arrows indicate cuticle of the hermaphrodite). (Scale bars. a,b,c—100 μm). ap—aperture of the male; nl—natatory limbs.

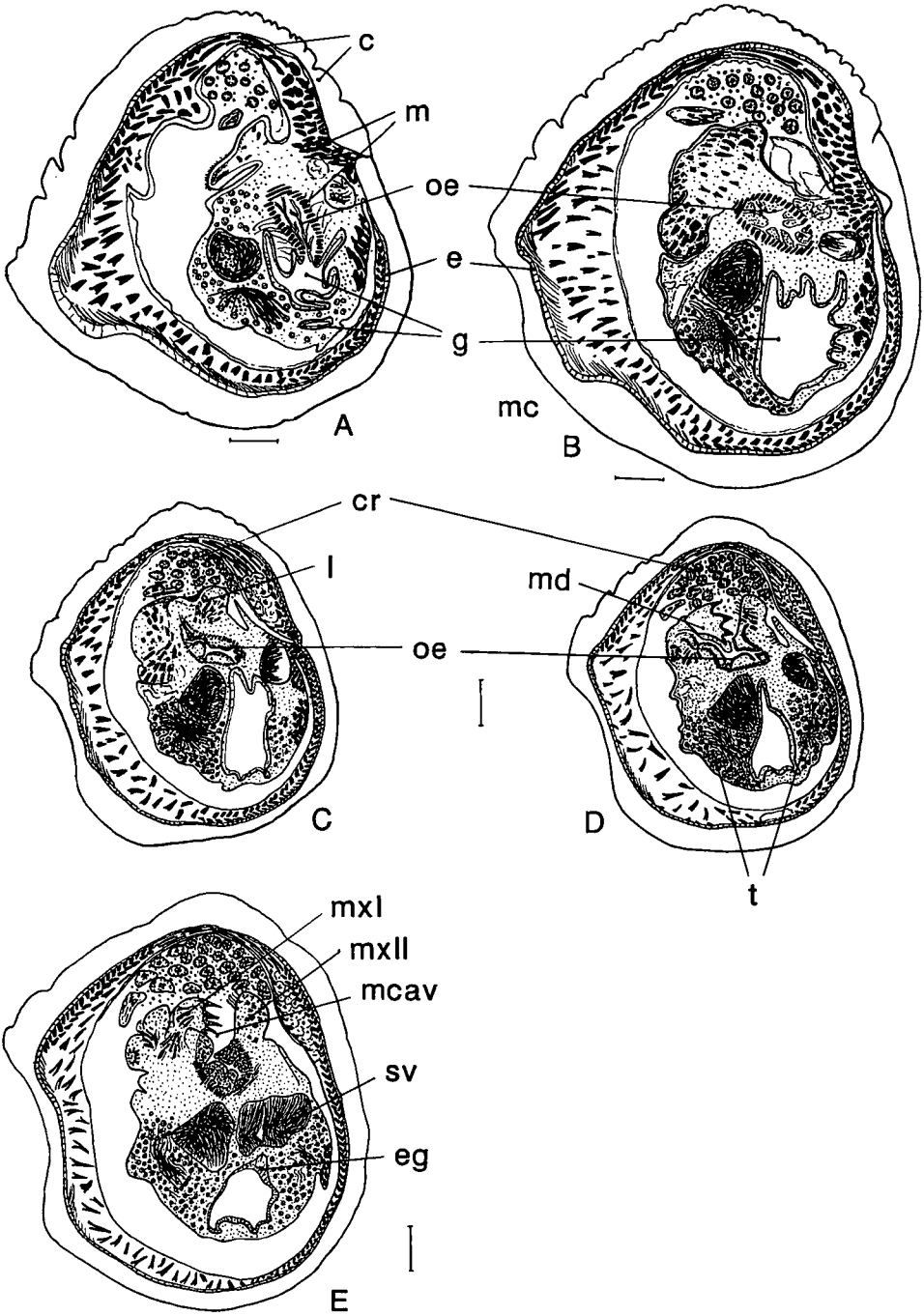

Figure 3. Semi-thin transversal sections of male: A,B—at the level under labrum; C—at the level of labrum; D—at the level of mandible; E—at the level of maxilla I. (c—cuticle; cu—cirri, caudal appendages and penis; e—epithelium of mantle; eg—epithelium of gut; g—gut; l—labrum; lp—labrum palps; m—muscles; mc—mantle cavity; md—mandible; mxI—maxilla I; oe—oesophagus; sv—seminal vesicles; t—testes). (Scale bars: A—90 μm; B—80 μm; C,D—114 μm; E—95 μm).

the crest and setae at distal margin; palps narrow, straight and covered by setae (Fig. 1K). Mandible with three sharp teeth, first tooth bearing sharp spines on lower side, second and third teeth almost completely covered by such spines; lower angle short, with four to five sharp spines, upper spine largest . Maxilla I with one large spine and two small spinules at upper angle, separated by distinct notch from third tooth; cutting edge and interior angle covered by setae. Cirri with normal anterior and posterior rami; setation acanthopod. Rami of cirri I with unequal rami of nine and seven wide segments, and single filamentary process at base of pedicle (Fig. 1E). Rami of cirri II–VI subequal, with 17 to 20 segments gradually narrowing distally. Caudal appendages longer than 0.5 length of cirrus VI, consist of 12 segments (Fig. 1m). Penis annulated, wide at base, less than 0.5 length of cirrus VI. AFFINITIES. This species shares a number of common characters with *P. xenophorae* (Annandale, 1905): 1. Both *P. klepalae* and *P. xenophorae* have a similar appearance, (construction of capitulum, orifice and peduncle and their dimensions); 2. Maxilla I has a distinct notch; 3. Both species inhabit *Xenophora* sp. and occur at similar depths. But there are some differences between *them:* (1) The cuticle of the new species *P. klepalae* is tuberculate; (2) The caudal appendages of *P. klepalae* are longer and have more segments; (3) the mandible bears more spines than in *P. xenophorae*; and (4) *P. klepalae* is from north of Madagascar while *P. xenophorae* ranges from southern India to Japan (Utinomi, 1958). *Paralepas klepalae* differs from *P. morula, P. tuberculata* and *P. modulosa* in having only rostral and carinal concentrations of tubericles while occupy all surfaces of capitulum in these species. No scuta and keels were found in investigated specimens as well.

The Male.—The cyprid larva (Figs. 1A,D; 2A,B) and the male (Figs. 1C; 2C), both are attached externally just below the orifice, and therefore we infer that the cyprid will become a complemental male. Appearance is similar to that of other cyprids of the Lepadomorpha. The cyprid was separated from adult and its external morphology investigated by means of light microscope is shown in Figure 2A,B. It measured 1.25 mm in length and 0.59 mm in height. After treatment of the larva in a solution of about 10% KOH, it could be observed that the thorax bears six pairs of biramous natatory limbs and the caudal appendages (Fig. 2B), as in ordinary cyprids. The complemental male, like the cyprid larva, was firmly attached to the same location on the hermaphrodite, and it could only be separated with part of cuticle of the hermaphrodite indicated by the arrows in Figures 2C. Its external morphology was examined by means of a light microscope. The body dimensions were diameter at the base: 900 μm, the maximum length: 800 μm. DESCRIPTION. Body globular, with color as in hermaphrodite. Cuticle about 50–100 μm thick (Figs. 3A–E), with small tuberculate formations, similar to those of hermaphroditic specimens. Distinct small aperture present at top of the capitulum; stalk absent. The internal morphology of the male was investigated using semi-thin sections (see Material and Methods). Beneath the cuticle there is a thin layer of hypodermal tissue, consisting of flat cells (Fig. 3A). A well-developed layer of striated, obliquely directed muscle fibers is present everywhere under the hypoderma. The mantle cavity developed and has a thin layer of cuticle inside, at the top part of body (Figs. 3A,B). CIRRI AND MOUTHPARTS. It is impossible to give a complete description of the cirri and mouthparts of the male, because we used of the semi-thin sections. It has six pairs of apparently normal, biramous cirri covered by setae, and a pair of caudal appendages (Figs. 3A–E). Mouthparts are also presumably developed 'normally' and resemble those of the hermaphrodite. There are labrum (Fig. 3C), mandibles (Fig. 3D), maxillae I (Fig. 3E) and

maxillae II (Fig. 3E). The cutting edges of mandibles and maxillae I bear well-developed teeth (probably three on the mandible) and there is a spacious gut (see below). Based on these observations, we can conclude that the cirri and mouthparts function normally. DIGESTIVE TRACT. The digestive tract consists of the mouth cavity (Fig. 3E), oesophagus (Figs. 3A–D), and well-developed gut (Figs. 3A–E). The mouth cavity is short and situated at the level of maxillae I–maxillae II. The lumen of oesophagus, as observed in the semi-thin sections, appears branched, with groups of secretory cells situated around. A layer of circular muscle surrounds the oesophagus. From the mouth cavity, the oesophagus curves upward and opens into the folding gut, at the level of labrum (Fig. 3A). The gut is well-developed, and folded strongly in the upper part; it has the form of an irregular tube in the middle and lower parts. The epithelium of gut consists of one layer of elongated secretory cells. We have observed undigested particles inside the gut. REPRODUCTIVE ORGANS. There are paired testes (Figs. 3A–E), seminal vesicles (Figs. 3A–E), and the ductus ejaculatorius of the penis. The testes together with the seminal vesicles constitute about 0.33–0.5 of the volume of the body proper where they are situated on either side of the gut. We have observed successive stages in spermatogenesis in the testes in the semi-thin sections. The seminal vesicles are closely pressed against the testis and their maximum diameter is about 20 μm. The penis is shortly than the length of the cirri; its maximum diameter is more than the basal diameter of the cirri. There were clusters of spermatozoa in the duct of the penis.

Etymology.—This species is named in the honor of Dr. Waltraud Klepal.

DISCUSSION

Klepal (1987) treats the morphology, evolution and phylogeny of all known cirriped males.

The male of *P. klepalae* is "complemental" (Darwin, 1851) because it is attached to the hermaphrodite, outside and rostral in position (Newman, 1980). Newman (1980) explained such positioning by males: "Since the very small male is permanently attached and transfers sperm by a probosciform penis, it must situate itself at some appropriate distance from the aperture of the mantle cavity of the hermaphrodite." While it is the first described in the Heteralepadidae, the apertural individuals of *Heteralepas vetula* Pilsbry illustrated by Pilsbry (1911, pl. XII, figs. 2,3) may also be males (Newman, pers. comm.).

The male of *P. klepalae* is similar to the males of *Scillaelepas, Calantica* and *Smilium* in having normal mouthparts and cirri and some armament of the capitulum. It is similar to the males of *Euscalpellum* and *Scalpellum* as well, in the absence of a stalk or peduncle, but the males of *Scalpellum,* at least, are without mouthparts and their cirri and digestive tract are reduced.

The significance of the male in the phylogeny of the Thoracica has involved the question of whether gonochorism or hermaphroditism was the original condition. Two different hypotheses exist. Several authors (Broch, 1922; Utinomi, 1958; Newman, Zullo and Withers, 1969) suppose the sexes were separate originally and that hermaphroditism is a secondary condition adapted to a fixed and gregarious mode of life. The fact that separate sexes are found in the Ascothoracica, Acrothoracica and relatively primitive Thoracica, and in the Maxillopoda, in general, support this supposition. Other authors consider hermaphroditism as the original condition in cirripedes (Darwin, 1851, 1854; Hoek, 1883; Foster, 1980; Newman, 1980; Moyse, 1983; Charnov, 1987). For example, Foster (1980) wrote "The Cirripedia may be fundamentally hermaphrodite, even though they

may have originally derived from the isomorphic dioecious condition of other Maxillopoda."

Probably, complemental males of cirripedes originated independently in the course of the evolution of this taxa. Some facts confirm it: among the family Scalpellidae, the most primitive genera such as *Lithotrya, Capitulum, Pollicipes* and *Neolepas* (Foster, 1978; Newman, 1979) include only hermaphrodites without males. Foster indicated that "more advanced genera like *Calantica* and *Smilium* have males... The phylogenetic trend shown in the scalpellids is towards an association with complemental males, perhaps facultative in calanticids (Foster, 1978) but obligatory for cross-fertilization in the 'higher' arcoscalpellids where the larger and more normal partner lacks a male reproductive system. If this is the correct sequence of evolution, and the phylogeny is compelling, then it follows that instances of complemental males in other families have been independently evolved."

It is obvious now that the complemental males of cirripeds originated due ecological conditions. For example, Newman (1980) writes "... what was the impetus for the development of complemental males in the first place? Where population densities of cross-fertilizing hermaphrodites are great, it is difficult to surmise what selective advantages there might be for the development and/or perpetuation of complemental males. However, if the probability of hermaphrodites being sufficiently close together to cross-fertilize became drastically diminished, the need for complemental males becomes obvious if the advantages of cross-fertilization are to be mentioned... Thoracican cirripeds, if not fundamentally hermaphroditic, became so early in their evolution. However, they are preadapted to the production of complemental males because their hermaphroditism is protandric... Thus, a cyprid that settles near an established hermaphrodite has the opportunity to act as a male before it becomes fully mature."

The occurrence of generalized complemental males in Balanomorpha (McLaughlin and Henry, 1972; Zevina and Polaykova, 1986; Foster, 1980; Dayton et al., 1982; Yamaguchi and Newman, 1990) also suggest the trend away from the hermaphrodite condition and towards the unisexual dioecious one due to ecological conditions. None the less, the present separate sexes in the Ascothoracica and the Acrothoracica suggests that perhaps gonochorism was the original condition for cirripedes. So, in some cases we cannot be sure, whether gonochorism or hermaphroditism was original for the present genus.

Males occur more often in the Scalpellomorpha than in the other thoracican subordes. They are sometimes characteristic of cirripedes inhabiting substrata with limited space, such as koleolepadids living between the pedal disc of an anemone and a gastropod shell inhabited by a hermit crab, and *P. klepalae* on *Xenophora.* In these cases presumably a gregarious mode of life is very difficult so the small complemental male has developed.

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